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A SCLEROTIOID DISEASE OF BEECH ROOTS.

BY HERMANN VON SCHRENK.

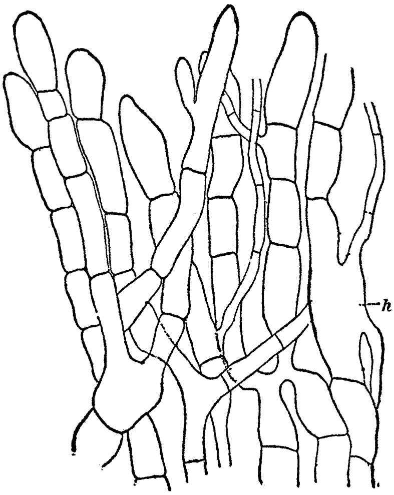
In the examination of some beech humus at Grand View, Rockland Co., N. Y., during the past summer, a large number of small tubercles were found attached to the fibrous roots of the beech trees. These trees grew in a clump, thirty or forty together, in a creek bottom in a rich humus soil, strongly admixed with clay. Cattle had cropped the ground closely, and had here and there wounded the larger surface roots. From such points numerous shoots had grown. A number of these were carefully dug up, to verify the connection of the tubercles with the beech roots. No tubercles were found on any beeches away from the clump mentioned. Masses of earth with roots and tubercles were collected and washed out, and the smaller roots with the attached tubercles were hardened in alcohol.

The tubercles were of various shapes and sizes, some almost round, others more elliptical or heart-shaped, and varying in size from those about as large as a small pea to some barely visible to the naked eye. Many occurred close together, oftentimes several on a small root (Pl. 55, fig. 1). Here and there one tubercle has the appearance of being composed of two or more parts (Fig. 1 'a', Fig. 2). From each body colorless strands extended through the ground, which join or pass from the tubercle at no definite point (Pl. 55, fig. 1 'b', fig. 2. Pl. 56, fig. 3 'b'). The tubercles are grayish-white in color.

With these bodies, others, very similar to these, are found. These are more regular in form, of a finer texture, and yellowish in color. On examination they proved to be small sclerotia, such as one frequently finds in humus soils.

They probably belong to some one of the Agaricinae. The sclerotia had no very definite outer layer, and were uniformly composed of very fine hyphae, loosely interwoven. Toward the periphery these became more or less parallel, and at certain points passed off in the form of long strands, resembling those passing off from the tubercles. Nowhere was any direct connection established between the two masses.

On examining the gray tubercles more in detail, they are found to consist of a bundle of cylindrical bodies, much intertwined, evidently roots, which are covered and firmly held in place by a membrane or sheath. The latter is composed of fungus hyphae, arranged in two distinct layers, easily to be torn one from the other. The sheath as a whole is but loosely connected with the bundle of roots, as very slight teasing with a needle will enable one to pull off the whole intact. With this sheath the strands of hyphae already mentioned are pulled off. Of the two layers, the outer is the thicker one. It is formed of hyphae parallel to each other, or nearly so, of a very large diameter and many-septate. The individual cells are about twice as long as they are broad, and in all cases are empty. The hyphae branch freely, and anastomose frequently with neighboring hyphae. One cell may have several branches (at 'h') either of the same diameter or smaller, one



HYPHAE FROM OUTER LAYER OF SHEATH (X520).

branch extending forward, the other back. H-connections are frequent, and once a distinct clamp cell was found. Because of this frequent branching and anastomosing, the whole layer is firmly united, and forms a mat, which no teasing can separate into its component threads. In section this layer appears like a layer of pseudoparenchyma (Pl. 55, fig. 8 'p'. Pl. 56, fig. 2 'p'), varying in thickness at different points on the tubercle. Wherever any depression on the latter occurs, the hyphae of this layer immediately fill it, so that in many places it is several millimeters in thickness. The inner layer (Pl. 55, fig. 8 's') is formed of very fine hyphae, so closely interwoven that it was not possible to separate the individual threads. The hyphae of this layer are easily torn, so that in pulling off the sheath, they readily separate from the main mass of hyphae and rootlets. The latter are firmly held in place by the hyphae (Pl. 56, fig. 2 'o'); which completely surround each root, and fill all spaces between them. Often, open spaces occur between the roots, crossed by strands of mycelium, looking as if the roots had spread apart, and had not yet given the fungus an opportunity to fill the space. Around a number of root tips two layers of fine hyphae are very evident (Pl. 55, fig. 10 'h'. Pl. 56, figs. 1 and 2 'h'). The layer which is next the tip, is much denser than the following one, and consequently darker.

Coming now to the main body of the tubercle, it is found to consist of a large number of small rootlets, much twisted and contorted, which, when the sheath is removed, present an appearance much like a mass of intestines (Pl. 56, fig. 3). They are firmly pressed one against the other, and are held in place by the fine hyphae. If they are torn apart and straightened out as far as possible, it is seen that these roots are branches and branchlets of a larger root, and apparently have all originated from a single root. A small piece of the large mass is represented, much flattened, on Pl. 55, fig. 10. Each branch is much bent from side to side, and looks as if some obstacle had been put in its path, and as if by a series of nutations it had endeavored to get away from the obstruction. At short intervals new branches appear, up to within a few millimeters of the root-tip. The branching is irregular, but the majority of the branchlets have a direction parallel to each other so that a longitudinal and transverse axis of each tubercle can be distinguished. If a longitudinal section be made through a tubercle some rootlets are cut transversely, but the majority in part radially and in part tangentially parallel to the longer axis. A complete radial section is impossible because of the contorted form of the roots. A section reconstructed from a large number of sections is represented on Pl. 56, fig. 1. It is to be noted that all roots keep on growing, even after giving off branches, so that on one transverse plane there are but few young roots (Pl. 55, fig. 10). A transverse section shows most of the roots cut across (Pl. 56, fig. 2). Between the roots the fine filling of fungus hyphae is seen, and about one, a darker ring ('h') indicating that this section has been made near the tip of the rootlet.

The structure of each root is peculiar. On the outside is an epidermal layer composed of elongated cells, looking much like palisade cells. These give one the impression that the root may have endeavored to get rid of the appressing fungus by increasing in diameter. Nowhere do any fungus threads enter this layer of cells. The hyphae lie closely appressed, and seem to adhere to the cell wall, but I never saw any of them penetrate it. Inside this epidermal layer come two layers of the cortex, the endodermis and two radial bundles (Pl. 55, fig. 8). There are no intercellular spaces, and the cell walls everywhere are very thin. The root tip is much simplified. The root cap consists of but two layers of flat cells (Pl. 55, fig. 9 'c') resembling in this respect the root cap of the mycorhiza. The large columnar epidermal cells originate close to the tip ('e'). The meristem cells are very large, compared with those found in the roots of the mycorhiza.

In tracing the development of these tubercles the structure of the beech roots as they are found normally must be remembered. Since the researches of Frank * it is generally recognized that the roots of the beech when grown in humus soil, are surrounded at their tips by a mantle of fungus threads, which grow in more or less intimate contact with the root itself, and, according to Frank, sustain a sort of symbiotic relationship, known collectively as the mycorhiza. But few of the fungi to which these hyphae are supposed to belong are known as yet, but wherever beeches occur in humus soils, some fungus is found associated with their roots.

This is true of our American beech, *Fagus ferruginea*, of which roots from different localities have been frequently examined. The roots of the mycorhiza are as a rule coralloid in form, i. e. short, frequently branching, grayish-white in color, but never, so far as I have seen them, contorted or hypertrophied in any way.

The trees at Grand View had no fungus mantle on the ultimate root tips of the larger roots on which tubercles were found. All rootlets free from the tubercles were short, with a blackened epidermis. All stages from such short uncovered roots to the full-sized tubercle were seen, and the method of growth appears to be as follows. The strands of some humus inhabiting fungus happen to grow over one of the ultimate branches of the beech root. For some reason the hyphae of that strand then develop profusely at the point of contact and gradually grow around the root. The beginning and end of the strand are soon not to be distinguished (Pl. 55, fig. 7) as its hyphae pass imperceptibly over into those of the forming sheath. It ought to be said that hyphae of large as well as those of small diameter are found in the strands passing about the beech roots. The sheath grows rapidly along the rootlet, until it reaches the point where that root joins a larger one. If another small root happens to be close by, the hyphae may grow over that one in similar manner, as evidently they did in several instances (Pl. 55, figs. 1 and 2). Shortly after being thus enveloped the rootlet begins to grow vigorously, at least it tries to. Lateral rootlets begin to appear close to the tip (Pl. 55, figs. 4 and 7 'b'), and they are pressed against the parent root by the enveloping sheath. In their endeavor to grow out, the roots execute circumnutating movements and gradually acquire the much contorted appearance already described. A number of stages in the process are shown in figs. 4, 5 and 6. Here the sheaths have been removed for clearness, and the branches have been pulled apart. Originally they were closely appressed. After some time the large skein is complete, and it is impossible to say how long the process would have continued. As each tubercle grew in size the enveloping hyphae kept pace with the growing roots. Sometimes two tubercles would touch, and then the hyphae of the two sheaths would fuse and thus bring about the appearance of a compound tubercle (Pl. 55, fig. 2).

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* **Frank, B. Über die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze. (Ber. d. deutsch. bot. Gesell. 3: 128. 1885.) — Über die physiologische Bedeutung der Mycorhiza. (Ber. d. deutsch. bot. Gesell. 6: 248. 1888.)**

It now remains to inquire what the cause and meaning of the formation of these structures may be. The beech roots are as a rule covered by a fungus mycelium, which surrounds them and of which many hyphae enter the epidermal cells. All observers, Frank,* Schlicht,† Sarauw,‡

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* Frank, B. *l. c.*

† Schlicht, Alb. Über neue Fälle von Symbiose der Pflanzenwurzeln mit Pilzen. (Ber. d. deutsch. bot. Gesell. **6**: 269. 1888.)

‡ Sarauw, G. F. L. Rodsymbiose og Mykorhizer saerlig hos Skovtraeerne. (Bot. Tidsskrift **18**: 127. 1893.)

Möbius,* and others agree that the only effect which the fungus has on the root is to stunt it, and as if to counterbalance this, it causes it to branch more frequently than it otherwise would. A multi-branched coralloid form of root is thus brought about. This has been one of the reasons for considering the relation of fungus and root a symbiotic one, for in cases of parasitism some form of hypertrophy, starch accumulation, or other evidence of stimulus is met with.† In the tubercles described there is evidently some form of stimulus which brings about the proliferation of roots, and that stimulus is probably exerted by the fungus mycelium. To that extent the phenomenon would lead one to class the structures among such as are formed because of the action of some parasitic fungus. But there is here no evidence of parasitism, no starch accumulation, and what is more, no evident connection between the fungus and the root. The hyphae simply surround the roots without entering the cells. Because of the greatly increased and abnormal growth of the roots, which cannot be without effect on their physiological activity, much less of benefit to them, one must class the tubercles as pathological conditions of these roots. The presence of a large number of small sclerotia together with the tubercles suggests that the sterile mycelium of the tubercles probably belongs to some Hymenomycete which usually forms sclerotia. Some of these hyphae come into contact with the beech roots, stimulate them, and then, in their further growth, adhere to the sclerotium-forming tendency and thus bring about the tubercles described. Their nearly constant form and size, as well as the similarity of the loose hyphal network with that of the small sclerotia all point in that direction.

The formation of numerous twisted roots with short branches is without doubt due to a stimulus exerted by the fungus. The only causes which could bring about advancement toward the root tips of lateral root-formation are two, pressure at the tip, and injury to the same, both equally effective in preventing onward growth of the root.* The experiments of Pfeffer and of Newcombe showed that growth had to cease entirely before the lateral roots make their appearance. Experiments of my own led to similar conclusions. Seedling beans, peas, cotton, squash, castor beans were grown in plaster, both completely hard, and softened plaster kept in moist chambers, solutions of gelatin, in rubber bags, etc. The results are to be recorded elsewhere. All the experiments showed conclusively that only when there was an absolute cessation of growth, did the lateral roots appear. The pressure must be a great one, which prevents onward growth, and it is scarcely conceivable that the pressure exerted by an envelope of fungus hyphae would be sufficiently great to do this. But aside from this the pressure, if such existed, did not stop the growth, for as has been said, the roots all kept on growing, even after being covered by the fungus sheath. It would then appear that the only other cause except that of stimulus, which would bring about lateral root development, could not have been effective in this case.

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* Möbius, M. Der Erdboden in Beziehung zur Ernährung der Pflanzen. (Gartenwelt **3**: 154. *fig. 1.* 1898.)

† Frank, B. Ber. d. deutsch. bot. Gesell. **3**: 258. 1885.

It is impossible to say what kind of fungus it was, which enveloped the roots, but it seems probable that it is distinct from those forming the mycorhiza. It is by no means a rare occurrence to find fungus mycelium about beech roots, which seems to have no connection with the same. Masses of roots collected at Oran, Mo., during October were almost white in color because of some fungus surrounding the roots like a fine web. The smaller roots were much contorted, and like those in the tubercles, but each rootlet was covered with a sheath of fungus mycelium, like that of the typical mycorhiza. It is difficult to say whether this mycelium was distinct from that of the mycorhiza. I am inclined to think that it was, as it occurred in isolated spots, and only among definite clumps of trees, while all trees of that locality had the mycorhiza form of root. The occurrence of so many forms of mycelia, some apparently closely associated with the roots, laying claim to symbiotic relationship, others evidently more distinct from the root, such as the one which formed the tubercles, suggests that the problem of the root fungi in relation to trees is still an open one.

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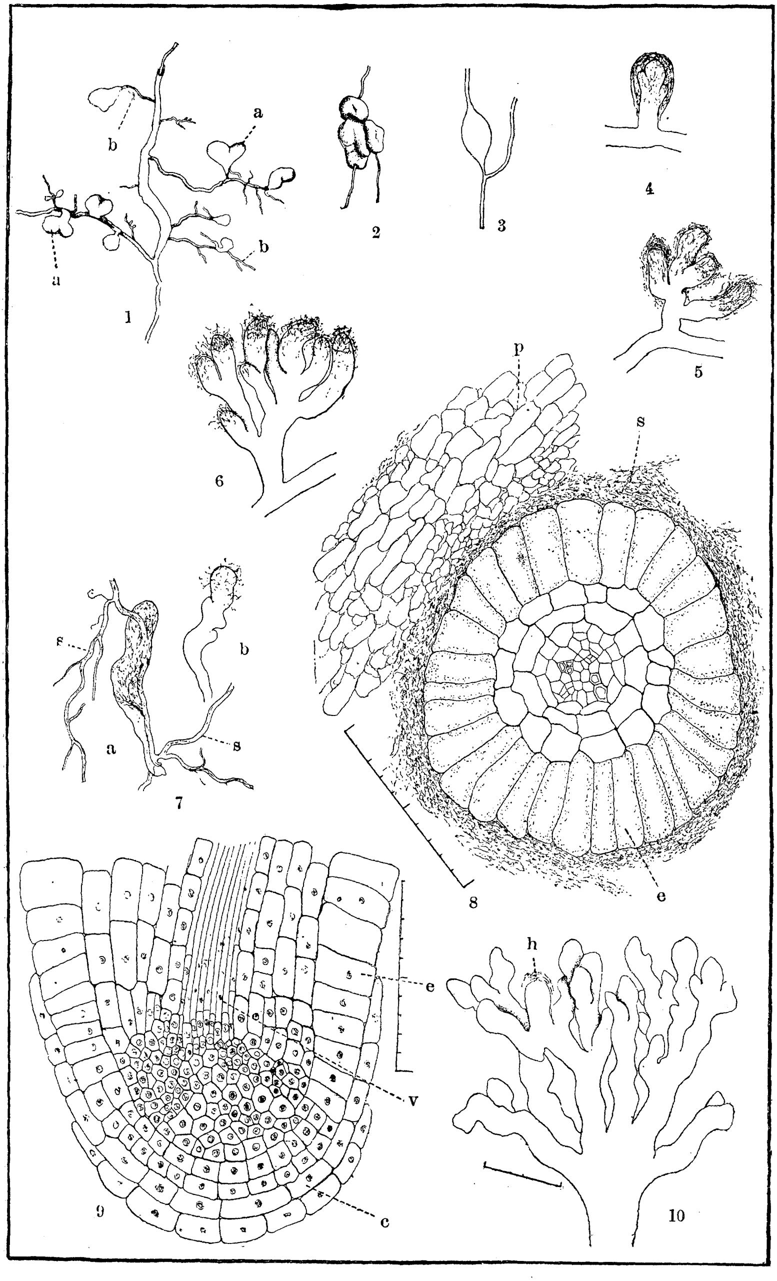
* Pfeffer, W. Druck und Arbeitsleistung durch wachsende Pflanzen. (Abh. d. könig. sächs. Ges. d. Wiss. **20**: 235–474. 1893.)—Newcombe, F. C. The influence of Mechanical Resistance on the Development and Life Period of Cells. (Bot. Gazette **19**: 149. 1894.)

EXPLANATION OF PLATES ILLUSTRATING SCLEROTIOID DISEASE OF BEECH ROOTS.

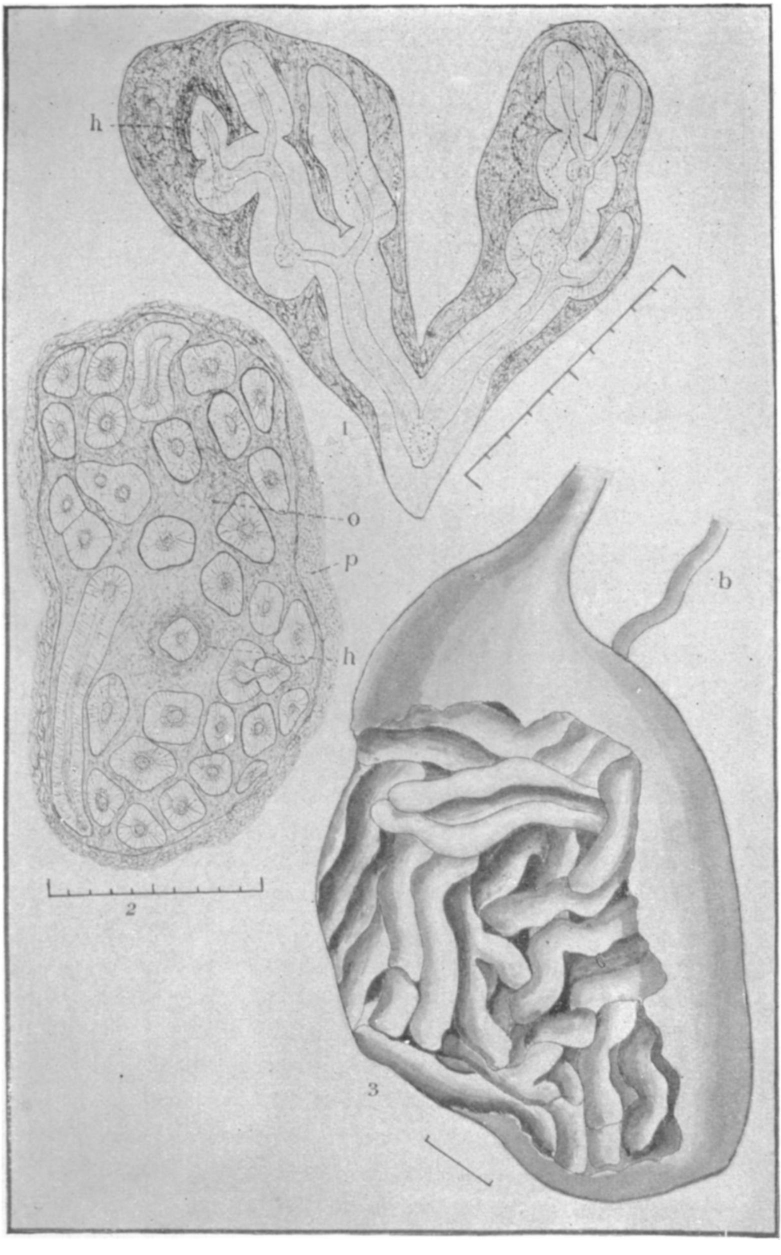
Plate 55. — 1, Beech root from Grand View, N. Y., showing sclerotioid bodies 'a' with fungus strands 'b' leading from each one (× 3). 2, Large tubercle, composed of three smaller ones, whose sheaths have united (× 1). The various depressions indicate separate masses of roots. A fungus strand comes from each mass. 3, A small sclerotium found near the beech roots (× 4). 4, Optical section of early stage of tubercle; covered with fungus sheath and showing two branches originating close to the root-tip (× 6). 5, An older stage of a tubercle (× 6). The fungus sheath has been removed, and the branches are spread out. Some of the fungus threads adhere to the roots. 6, Still more advanced stage, roots spread out (× 6). 7, a, The beginning of a tubercle, 's' fungus strands growing over a root, and spreading out forming a sheath (× 7); b, sheath removed, showing three branches just appearing (× 7). 8, Transection of root from tubercle, with a portion of the sheath; 'p' outer layer of sheath, composed of fungus threads of large diameter; 's' inner layer of sheath; 'e' epidermis of root. 9, Longisection through tip of root, slightly diagrammatic; the enveloping fungus hyphae have been omitted; 'c' two-layered root cap; 'e' epidermis; 'v' plerome cylinder. 10, A small portion of roots from a tubercle. Each branch keeps on growing, and forms branches constantly. The line at the side equals 2 millimeters; 'h' double layer of fungus hyphae around the root-tip.

Plate 56. — 1, Longisection of a young tubercle, reconstructed from

25 sections. Two adjacent rootlets have been covered by the fungus. 2, Transection of tubercle. All roots but two are cut transversely; 'h' double layer of hyphae; 'p' outer layer of sheath; 'o' mass of fine fungus threads surrounding each root and holding it in place. 3, Small tubercle, from which the fungus sheath has been partially removed, exposing the coiled mass of rootlets lying underneath; 'b' the strand from which the sheath developed. The line at the side equals 1 millimeter.



SCLEROTIOID DISEASE OF BEECH ROOTS.



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